Ecological functions, water quality, and management considerations in intermittent streams

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Intermittently flowing stream channels are an important feature in many landscapes, directing both short-term runoff and longer-term, near-surface flows into larger, more permanent channels. As such, their water quality is highly variable ranging from near rainwater in bedrock-lined localities to being laden with nutrients and tannins where flow reconnects stagnant, leaf-filled pools left over from previous precipitation events. Despite their ephemeral nature, intermittent streams support a diverse and often abundant flora and fauna, that latter comprising both invertebrates and fishes. Whereas some taxa are shared with permanent streams and rivers, others are restricted to intermittent waters where they demonstrate a range of interesting physiological and behavioural adaptations that ensures their survival. Amongst the biota are rare species whose conservation must be addressed in any management activity that seeks to alter natural flow regimes. Species whose metapopulations span both permanent and intermittent waters may have larger gene pools which may enhance their ability to cope with future changes to global environments.

From a hydrological perspective, intermittently flowing stream channels are an important feature in many landscapes, directing both short-term runoff and longer-term, near-surface flows into larger, more permanent channels. From a habitat perspective, intermittent streams strictly are defined as those which contain water on a cyclical basis, and where the dry phase is more or less predictable both in its time of onset and duration

This sets them apart from the more flashy episodic streams which contain water largely on an unpredictable basis (Comin and Williams 1994, Williams 1996).

There are very few estimates as to how common intermittent streams are in the landscape; at best they are indicated on topographical maps as thin, blue dotted lines

Such quantification would seem a necessary first step in gauging their importance as habitats. In England and Wales, a 1920s survey of both permanent and temporary ponds (applying a correction factor for ponds smaller than 6 m in diameter) showed a range from 0.12 km^{-2} in mountainous areas to 115 km^{-2} in areas of ancient woodland and agriculture (Rackham 1986). A preliminary survey of some 1:50,000 topographical maps of mixed rural and woodland areas in southern and central Ontario, Canada, shows densities of intermittent streams ranging from 43 to 582 per 540 km^2 (0.08 to 1.08 km^{-2}). On average, 85.3% of all first order streams shown on these maps are marked as being intermittent at their source. This value dropped to 13.0% on maps of heavily forested areas where many streams are marsh fed. Clearly, regions differing in geomorphology, vegetation, precipitation pattern, and underlying hydrology support different densities of intermittent streams, nevertheless these figures serve as a useful snapshot.

Frequency of occurrence of intermittent streams in southern and central Ontario, Canada

Area	Map scale	Map area	No. intermittent	No. permanent	% intermittent
Rural & woodland:					
Brampton	1:50,000	540 km^2	570	95	85.7
Alliston	1:50,000	540 km^2	43	8	84.3
Bolton	1:50,000	540 km^2	582	117	83.3
Barrie	1:50,000	540 km^2	87	10	89.7
Markham	1:50,000	540 km^2	363	73	83.3
Forested:					
Haliburton	1:50,000	540 km^2	29	78	24.8
Kawagama	1:50,000	540 km^2	27	86	23.9
Algonquin	1:50,000	540 km^2	25	125	16.7
Coe Hill	1:50,000	540 km^2	0	208	0*
Gravenhurst	1:50,000	540 km^2	0	326	0**

[* 64% and ** 83% of the streams were marsh-fed]

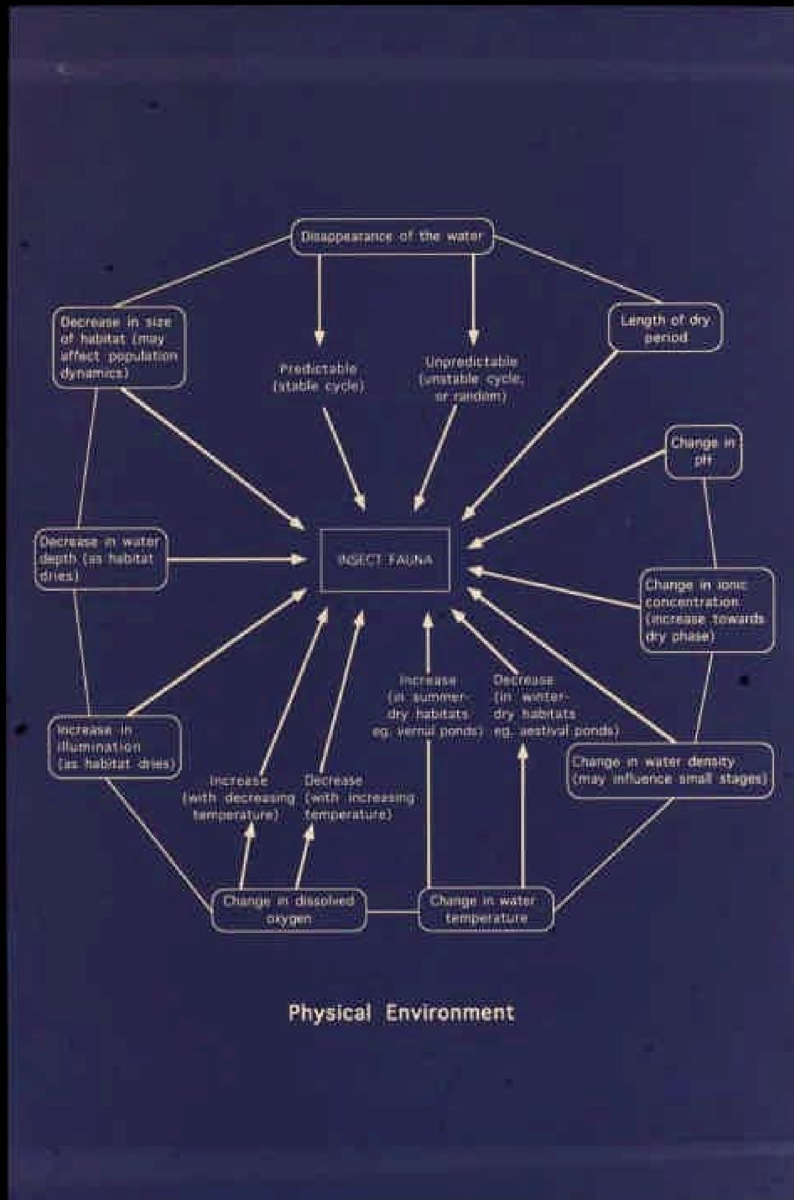
The physical and chemical natures of the intermittent stream environment typically fluctuate more than those of adjacent permanent streams and, as the aquatic phase draws to a close, frequently the habitat cyclically assumes semi-terrestrial characteristics [SLIDE 6], and finally fully terrestrial characteristics. Flow, for example, may be sustained at high levels (> 1m sec^{-1}) during snow melt or monsoons, but range down to zero at other times of year.

Consequently, water quality may be highly variable - ranging from near rainwater in bedrock-lined localities to being laden with nutrients and tannins where flow reconnects stagnant, leaf-filled pools left over from previous precipitation events

The Physical Environment

Major influences in the physical environment, together with pertinent interactive effects, are summarised in the next slide. Of fundamental importance is the pattern of disappearance of the water, whether predictable or unpredictable. Linked to disappearance of the water is the length of the dry period and decrease in habitat size (area and depth). Decreasing depth may increase in isolation which, through changes in primary production and wind-induced aeration, may change dissolved oxygen concentrations in the water. Primary production also may be affected by changes in turbidity. Oxygen will be further affected by changes in water temperature which will increase as the water disappears in summer-dry streams, but will decrease in winter-dry streams. Temperature changes result in subtle changes in water density which may affect the smaller life cycle stages of the biota. Ionic concentration tends to rise significantly as intermittent streams dry out; this may affect pH and perhaps have direct osmotic consequences for the biota, too. Water chemistry is likely to have a major influence on the biota but, apart from aspects related to dissolved oxygen and pH, has been poorly studied. However, leachates from newly inundated riparian leaf litter are likely to promote changes in water chemistry, and the release of tannins has been shown to inhibit feeding, causing high mortality, in some crustaceans (Cameron and LaPoint 1978). The implications of the addition of beneficial leachate materials, such as proteins and carbohydrates, from riparian litter are unknown but perhaps they parallel those known for permanent fresh waters (see review by Lush 1981). The impact of such processes will be related to local patterns of leaf fall in conjunction with the timing of inundation and the prevailing discharge. Nutrient input from subsurface (hyporheic) connections with permanent, interstitial water bodies has been shown to influence the algal growth in an intermittent stream with obvious consequences for benthic herbivores (Valett et al. 1994).

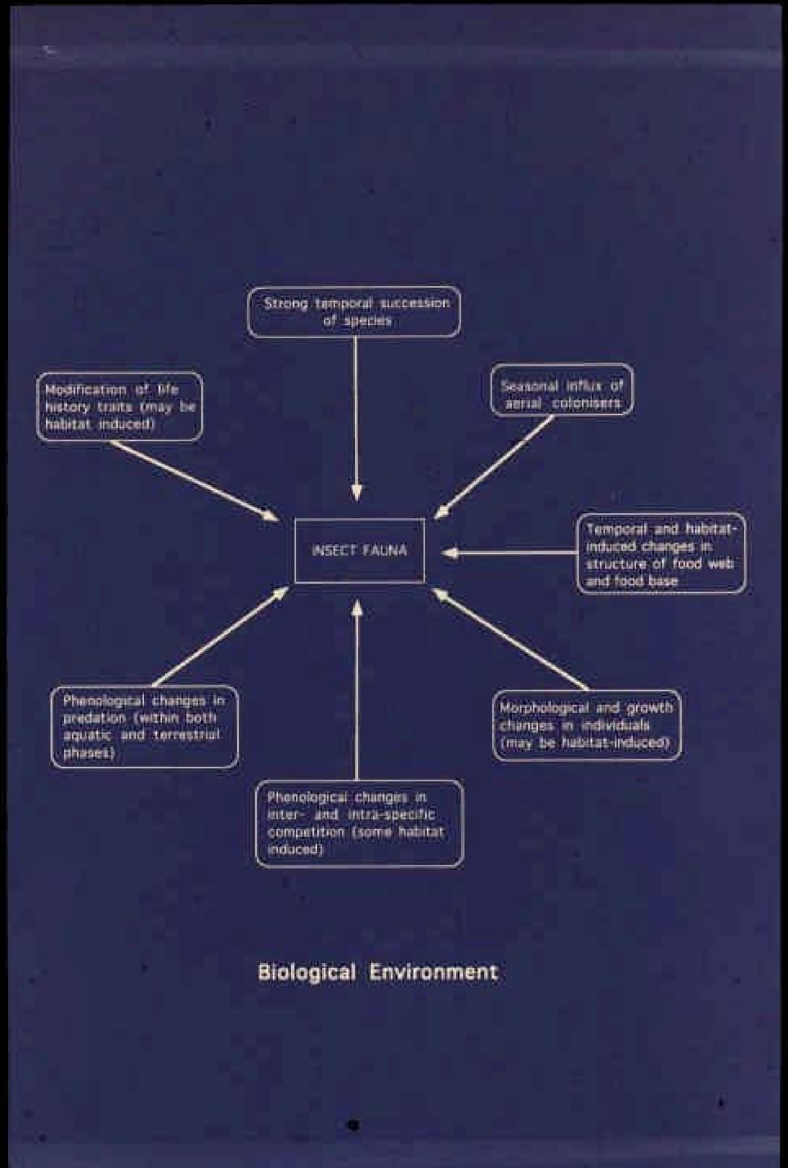
In intermittent streams, there are a number of discharge-related factors (e.g., temporal pattern, maxima-minima) that influence the biota both directly and indirectly, the latter through correlation with several of the other physicochemical factors shown in the model (Boulton and Lake 1990). The size and type of bed substrate particles are likely to exert influences ranging from suitability as attachment sites during the wet phase to protection from desiccation during drought (Boulton 1989).


Disappearance of the water
Decrease in size of habitat (may affect population dynamics)
Predictable (stable cycle)
Unpredictable (unstable cycle, or random)
Length of dry period
Change in pH
Decrease in water depth (as habitat dries)
INSECT FAUNA
Change in ionic concentration (increase towards dry phase)
Increase (in summer-dry habitats eg. vernal ponds)
Decrease (in winter-dry habitats eg. aestival ponds)
Increase in illumination (as habitat dries)
Change in water density (may influence small stages)
Increase (with decreasing temperature)
Decrease (with increasing temperature)
Change in dissolved oxygen
Change in water temperature
Physical Environment

The Biological Environment

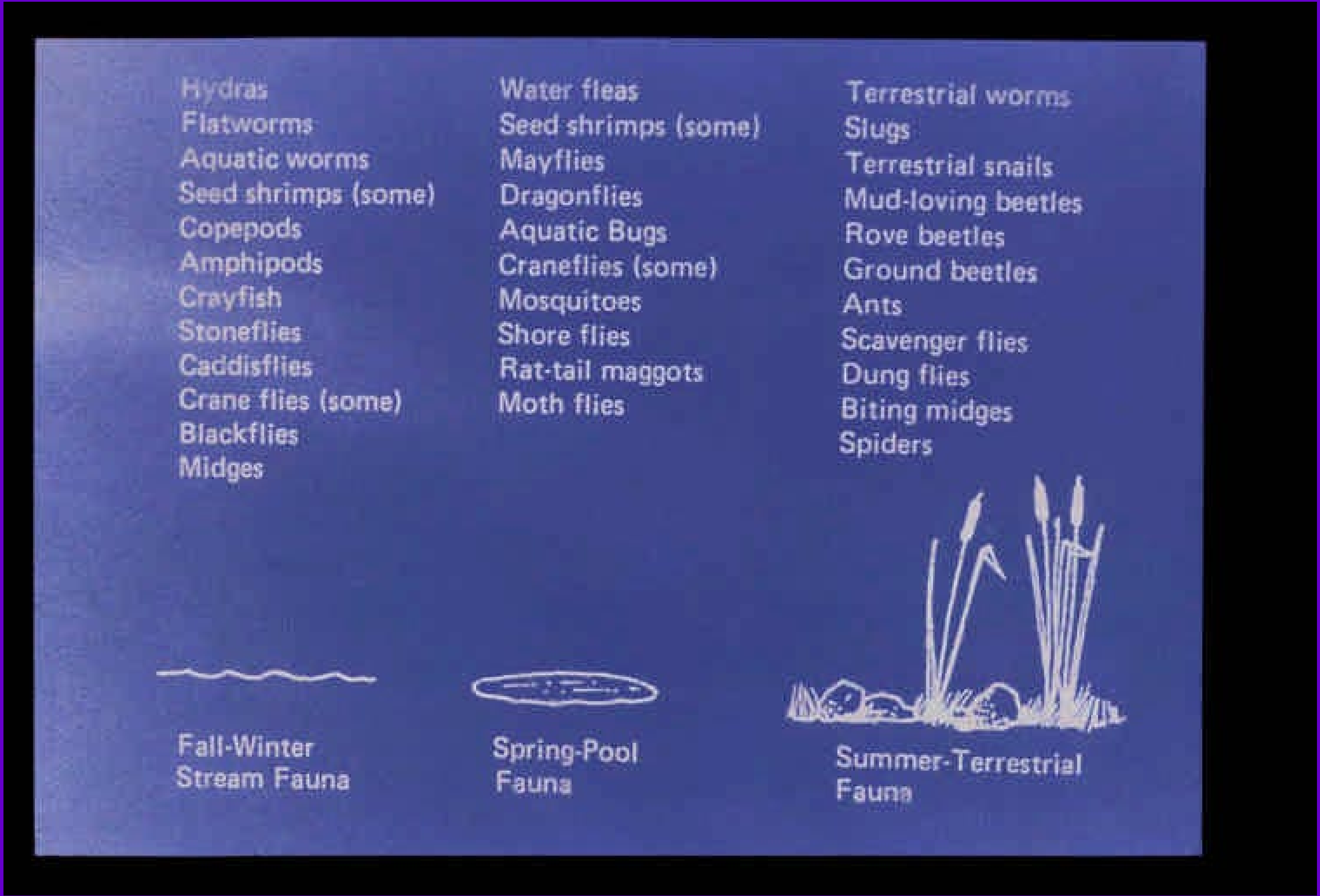
Features of the biological environment are summarised in the next slide. Whereas it is not difficult to identify the influence of single biological factors, assessing their relative importance and linkage is less easy owing to lack of research specifically on temporary waters. Strong biological features include the succession of species so characteristic of temporary waters (e.g., Williams 1983, Jeffries 1994), seasonal influx of aerial colonisers (Fernando 1958, Nilsson and Svensson 1994), and temporal changes in the food base - as surplus bed nutrients from the dry phase are used up, fungal and other decomposers process allochthonous bed materials, and phyto- and zooplankton become established (Bérlocher et al. 1978, Wiggins et al. 1980, Maher and Carpenter 1984). As a result of changes in the food base, together with variation in the numbers of predators (both as aquatic species succeed each other and as terrestrial ones invade the shrinking habitat), the structure of the food web must be subject to change. So, too, will the extent and intensity of inter- and intraspecific competition (Morin et al. 1988, Johansson 1993), although it has been argued that, in general, biotic interactions may contribute relatively little to community structure given the demanding requirements of the physicochemical environment (Poff and Ward 1989). In addition, a number of changes affect individual species, such as modification of growth, morphology and life history (Harrison 1980, Landin 1980, Juliano and Stoffregen 1994), that may be classed as genotype-environment interactions.

Strongly influencing community structure, indirectly and especially through trophic processes, will be many of the physicochemical factors already considered. However, from this suite of factors, habitat duration (length of the aquatic phase) is emerging as being perhaps the most important. For example, in a study of the relative influences on the invertebrate community of a Sonoran Desert stream, the dry phase was deemed to be more important than spates (Boulton et al. 1992), although floods may increase in influence as intermittency becomes less prolonged (Poff and Ward 1989). Further, Schneider and Frost (1996) concluded that the processes structuring temporary pond communities in Wisconsin were hierarchically organised by habitat duration.



Strong temporal succession of species
Modification of life history traits (may be habitat induced)
Seasonal influx of aerial colonisers
INSECT FAUNA
Temporal and habitat-induced changes in structure of food web and food base
Phenological changes in predation (within both aquatic and terrestrial phases)
Morphological and growth changes in individuals (may be habitat-induced)
Phenological changes in inter- and intra-specific competition (some habitat induced)
Biological Environment

Who lives there? The animals species that live in intermittent streams will tend to vary with stream size, the length of the hydroperiod and geographic location, although the presence of certain taxonomic groups is predictable. This next is an example of those taxa likely to be found in a small (1 m wide) temporary stream in northeastern North America (Williams and Hynes 1976). The fauna can be divided into three successive groups based on the water conditions found throughout the year. Inclusion in a particular group indicates that this is where the taxon passes the most active stages of its life.



The fall-winter stream fauna consists of those animals such as flatworms, amphipods and caddisflies which appear shortly after the stream starts flowing in the autumn and most have reproduced successfully before the flow stops in the spring.

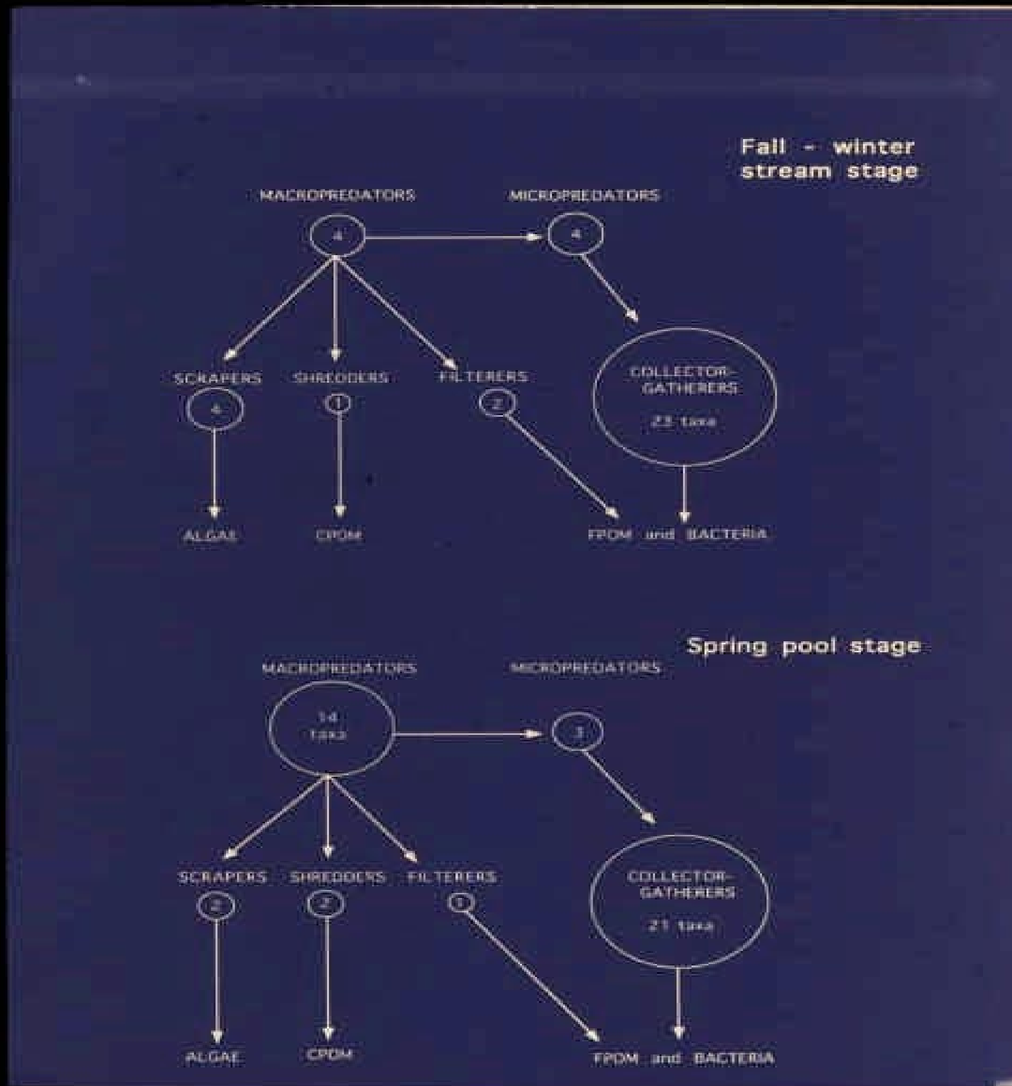
The spring-pool fauna represents those species that waited until the stream had stopped flowing and only shallow pools remained. These pools are excellent breeding environments due to the ease with which they warm up and the abundant plant food that develops in them. Some taxa, such as mosquitoes, may have been present as eggs during the stream stage, whereas others, such as the bugs and beetles fly in from nearby habitats, feed, lay eggs and raise a new generation of larvae which emerge before the pools dry up.

The summer-terrestrial fauna consists mostly of riparian species tat move onto the streambed once it has dried. Earthworms are probably attracted by the dampness, slugs, snails and some types of flies feed on stranded algal mats, and beetles, ants and spiders scavenge the bed for individuals left over from the aquatic phase.

Intermittent streams also may support several fish species. For example, 12 of the 50 species of fish found in the Grand River watershed, Ontario, were found in intermittent streams connected to the main channels (Williams and Coad 1979). White sucker and creek chub moved into the streams to feed and spawn, probably attracted by earlier breeding opportunities and reduced predation. The brook stickleback and various minnows may have been attracted by the invertebrate food, and were extremely tolerant of degraded water conditions towards the end of the aquatic phase.

Faunal dynamics:

There is sufficient replacement of species throughout these three stream stages that the structure of the faunal community differs substantially over time. Similar successions of species have been recorded in semi-arid foothill streams in central California (Abell 1984), in a desert stream in central Arizona (Boulton et al. 1992), and in two streams in southern Australia (Boulton and Lake 1992). Despite the obvious conclusion that such structural changes must be accompanied by functional changes in the community, very few quantitative attempts have been made to address the latter. Assignment of species in Kirkland Creek, Ontario, to major functional feeding groups illustrates these changes in the next slide Compared with the fall-winter running water stage, which is dominated by collector-gatherers, the spring pool stage shows a marked increase in macropredators - primarily due to aerial colonisation by adult beetles and bugs. Both adults and their offspring prey on members of the aquatic community. In two intermittent streams in Australia, predator numbers also peaked before the habitat dried; scraper densities rose in the late spring/early summer coincident with increased periphyton growth; and collector-gatherers and collector-scrapers were well-represented throughout the year (Boulton and Lake 1992).


Fall - winter stream stage
MACROPREDATORS
4
MICROPREDATORS
4
SCRAPERS
4
SHREDDERS
1
FILTERERS
2
COLLECTOR-GATHERERS
23 taxa
ALGAE
CPOM
FPOM and BACTERIA
Spring pool stage
MACROPREDATORS
14 taxa
MICROPREDATORS
3
SCRAPERS
2
SHREDDERS
2
FILTERERS
1
COLLECTOR-GATHERERS
21 taxa
ALGAE
CPOM
FPOM and BACTERIA

Special Adaptations

The loss of water from temporary habitats imposes a potential catastrophe on aquatic fauna. Intermittent stream insects, for example, have countered this "terrestrialisation" of their habitat by means of:

- Physiological tolerance
- Migration
- Life history modification.

Although the adaptations shown by individual species are varied, members of the same major taxonomic groups tend to employ similar stages in their life cycles. For example, mayflies, dragonflies, and mosquitoes largely survive drought as eggs (Lehmkuhl 1973, Ingram 1976, Wood et al. 1979), many beetles and bugs (Hemiptera) survive as adults (Macan 1939, Nilsson and Svensson 1994), and stoneflies survive as diapausing early instar nymphs (Harper and Hynes 1970). Midges (Chironomidae) may diapause as larvae or eggs (Thienemann 1954, Williams and Hynes 1977).

Physiological tolerance:

Frequently involves some form of diapause during the stage in the life cycle which coincides with the drought.

In its simplest form, arrested or retarded growth may result as a direct consequence of water loss from the organism's tissues. The animal thus becomes dormant when dehydrated but resumes growth when water is restored.

In other cases, there is a more programmed arrest of development for which a formal set of criteria is required before growth can continue.

Such a mechanism clearly has a safety feature built into it to prevent premature resumption of growth before the water in the pond is fully restored.

Active seasonal migration necessitates substantial powers of flight, coupled with mechanisms for locating and evaluating new bodies of water. It has been studied most in the bugs and beetles, and timing is very important in the process. Typically, adults having overwintered in some permanent body of water, disperse in early spring in search of newly-formed ponds. Here, eggs are laid and the young grow quickly under conditions of plentiful food and reduced competition. Adults of this new generation mature shortly before the dry phase and fly to new overwintering habitats in a second dispersal in summer (Fernando and Galbraith 1973). Some caddisflies are known to fly away from drying streams to hibernate in nearby caves. When flow resumes, they return to lay their eggs (Bouvet 1977). One study has shown that all of the dominant insects (beetles, corixids, and several dipterans) living in a seasonally flooded marsh persisted through repeated colonisation from nearby permanent habitats, rather than by physiological tolerance (Batzer and Resh 1992).

Migration

Is divisible into two forms, *active* and *passive*.

Active seasonal migration, seen mostly in insects, necessitates substantial powers of flight, coupled with mechanisms for locating and evaluating new bodies of water. It has been studied most in Hemiptera and Coeloptera, and timing is very important in the process.

Passive migration is seen typically in small species that do not have the capacity to migrate unassisted. Whereas this introduces a greater element of chance into successfully colonising new ponds, the odds generally are increased through, depending on species:

• production of large numbers of disseminules, frequently as dormant, drought-resistant eggs or reduction bodies that may dispersed by winds or by surface water drainage; or

• synchronisation of the life cycle with that of an actively migrating vector species.

Taxa that employ the first method include freshwater sponges (as gemmules), bryozoans (as encapsulated dormant buds, called statoblasts), tardigrades (as tuns), rotifers, branchiopods, copepods, and turbellarians (as resting eggs).

Taxa that use vectors may be transported either externally or internally.

Life history modification:

in aquatic insects is influenced by both internal factors (such as physiology, behaviour, and morphology), which tend to restrict life history traits within certain genetically pre-determined ranges, and factors in the environment (such as water loss, temperature, food, photoperiod, and other biota) some of which also can impose range limits (reviewed by Williams 1991).

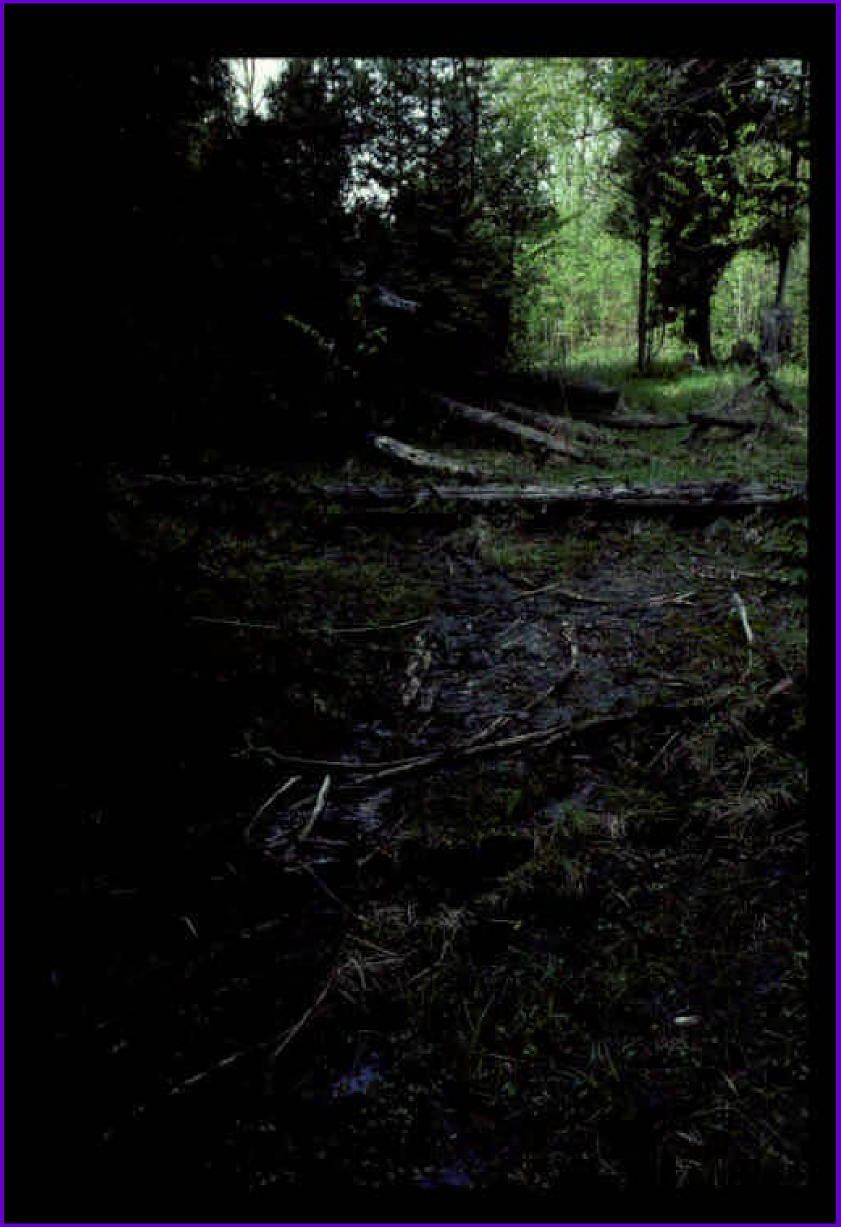
For the most part, the insects of temporary waters exhibit traits of r-selected species (sensu MacArthur and Wilson 1967), especially high powers of dispersal, rapid growth, short life-span, small size, and opportunistic/generalistic feeding, although comprehensive dietary studies are rare.

On the negative side, they may suffer from poor competitive abilities (e.g. McLachlan 1993).

Metapopulations, rare species and their conservation:

The cyclical nature of the intermittent stream environment creates a habitat that is quite distinct from that found in permanent streams. It is distinctive enough to support a fauna that contains elements that either are not found in any other habitat types or have their greatest populations in intermittent streams. In terms of contributing to a region's overall invertebrate biodiversity, therefore, intermittent streams are of considerable importance. This importance may be manifest also by maximising the gene pool of species that occur in both intermittent and permanent waters. For example, species that have populations in both might be expected, because of increased fitness demands, to have greater genetic diversity than species inhabiting only permanent streams. Increased diversity may be crucial to the survival of some species faced with possible future changes to global environments, such as may result from global warming (Hogg and Williams 1996). The consequences of decreased genetic diversity include the extinction of locally adapted populations with possible loss of alleles from a species' gene pool - this, in turn, may further reduce the species' ability to track future environmental change. In the global warming scenario, it is forecast that the impact will be most severe in northern latitudes (Hengeveld 1990).

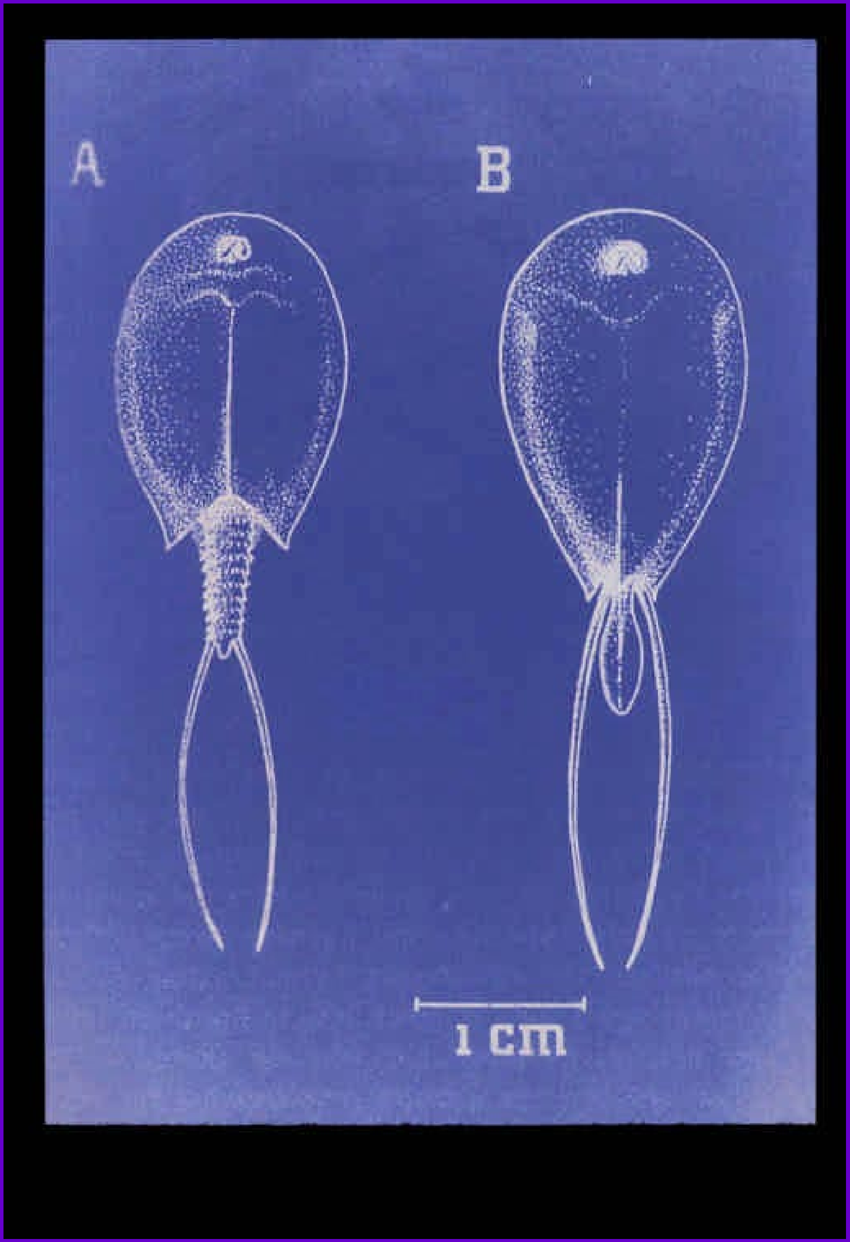
As genetic diversity is often lowest at the edges of a species' range, especially in northern latitudes (Sweeney et al. 1992), such populations will be the most likely to experience the greatest environmental change in the next few decades, yet may be among the least able to adapt. These potential consequences led Hogg et al. (1995) to urge aquatic biologists and conservationists to consider the evolutionary as well as the ecological consequences of habitat alteration. Once genetic diversity has been lost for a given species it may not easily be regained, even if pristine environmental conditions are restored.



Many temporary water habitats represent stages in the hydroseral succession of wetlands to more terrestrial habitats. This results from an excess production and accumulation of organic (largely plant) matter faster than it can be degraded. At a certain point in this transition, previously permanent waters become intermittent and eventually episodic. The process is entirely natural and as the water regime changes so do both the aquatic/emergent vegetation and the invertebrate fauna (see Wrubleski 1987).

Unfortunately, in many rural areas, the increased pressure of agriculture often leads to large-scale land drainage in an attempt to bring so-called "marginal" wetlands into cultivation. To do this, below-ground tile systems are installed with the expressed purpose of lowering the local groundwater table. Such practices destroy temporary water habitats and their associated biotas quickly and permanently, and should be discouraged. In Britain, lowering of water tables under the guise of land improvement is believed to have resulted in the extinction and near-extinction of two damselfies, Coenagrion armatum and Lestes dryas, respectively (Moore 1976; 1980). Moreover, the effects may extend to non-aquatic invertebrates that require wetland habitats. For example, drainage of fenlands has been cited as the reason for the loss of the Large Copper butterfly, Lycaena d. dispar and the dramatic reduction in Mole cricket, Gryllotalpa gryllotalpa, populations in England (Duffey 1968; Wells et al. 1983). In the southeastern United States, 40-50% of the formerly rich (> 1,000 species) freshwater molluscan fauna has been driven to extinction, or made endangered, as a direct result of drainage alteration (Stansbery, 1971). The magnitude of the latter loss in biodiversity has subsequently resulted in several conservation measures including: identification of endangered species and establishment of recovery programmes; development of methods for creating new habitat or relocating species; and the declaration of sanctuaries (Clarke 1981).

Protective legislation would seem to be an obvious solution, however an example from California serves as a warning. Lepidurus packardi [SLIDE 19], the vernal pool tadpole shrimp, is known only from CaliforniaÍs Central Valley and from a few locations in the San Francisco Bay area. Because loss of vernal pool habitat in California's Central Valley is estimated at between 65 and 90% of its former extent - due to urbanisation of flat lands (slope ~ 3-4%) close to metropolitan areas - in 1994 this species was designated as endangered and protected by federal law (Goettle 2000). In 1996, agricultural and business groups asked for delisting of two of the four species of endangered vernal pool shrimp, and are currently in the process of suing the U.S. Fish and Wildlife Service over the matter claiming that protection of the shrimp is a surrogate for land-use control (Evans 2000). Another example of lack of public sympathy for the fate of these shrimp is the fact that in California rice fields, Triops are looked on as pest species as they are reported to uproot and eat young rice plants (Fry and Mulla 1992).



In some cases, judgement based on habitat size rather than importance has failed to protect species. For example, small, isolated wetlands, such as are found in the southeastern Coastal Plain of the U.S., lack the legal protection given to riparian and lacustrine wetlands. Indeed, the U.S. Army Corps of Engineers permits wetlands less than 0.12 ha to be filled on an ad hoc basis, and requires only a minimal review of circumstances if they do not exceed 1.2 ha (Federal Register 1996). As a result of uncontrolled agricultural conversion and regional development, loss of these habitats and their unique faunas is escalating (Kirkman et al. 1999).

Management considerations:

(1) temporary waters, be they streams, ponds, pools, or wetlands are not “wasted” areas of land; they are natural features of the environment representing distinct and unique habitats often for endangered species;

(2) there is a strong likelihood that temporary waters contribute to maximising the gene pool of certain species that occur in both temporary and permanent waters and that this increased diversity may be crucial to the survival of species facing future changes to global environments. It is important, therefore, that scientists, managers and developers consider the *evolutionary* as well as the *ecological* consequences of habitat destruction or alteration;

Management considerations (contd.):

(3) a diversity of temporary water habitats exists in nature, particularly with respect to the length of the hydroperiod and size of basin/channel, and that maximum species diversity is best achieved by conserving a range of natural drought regimes in a variety of environments across wide geographical, physiographical, and climate conditions;

(4) the current state of knowledge of the biology and ecology of temporary water plants and animals is meagre, as is how species will react to contemporary changes in global climate. Regional development issues therefore require some indulgence, even if this means enactment of overly protective legislation, to allow the knowledge base to catch up so that species and their environmental role are not lost before their importance is understood.

Alongside these issues is the need, as recently emphasised by Everard et al. (1999), for an intensified “gentle education” of the public about temporary water environments so that an awareness of the collective ownership of ponds and small streams takes hold. In this way, a “bottom-up” process may develop that will temper the ravages that current “top-down” directives have wrought upon these habitats and their biotas.

References:

ABELL, D. L. 1984. Benthic invertebrates of some California intermittent streams. Pages 46-60 in S. Jain and P. Moyle (editors). Vernal pools and intermittent streams. University of California, Davis Institute of Ecology Publication 28, Davis, California.

BÉRLOCHER, F., R. J. MACKAY, AND G. B. WIGGINS. 1978. Detritus processing in a temporary vernal pool in southern Ontario. Archives fÄr Hydrobiologie 81: 269-295.

BATZER, D. P. AND V. H. RESH. 1992. Macroinvertebrates of a California seasonal wetland and responses to experimental habitat manipulation. Wetlands 12:1-7.

BOULTON, A. J. 1989. Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. Transactions of the Royal Society of Southern Australia 113:23-34.

BOULTON, A. J., AND P. S. LAKE. 1990. The ecology of two intermittent streams in Victoria, Australia. I. Multivariate analyses of physicochemical features. Freshwater Biology 24:123-141.

BOULTON, A. J., AND P. S. LAKE. 1992. The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. Freshwater Biology 27:123-138.

BOULTON, A. J., C. G. PETERSON, N. B. GRIMM, AND S. G. FISHER. 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. Ecology 73:2192-2207.

BOUVET, Y. 1977. Adaptations physiologiques et compartmentales des Stenophylax (Limnephilidae) aux eaux temporaires. Pages 117-119 in M.I. Crichton (editor). Proceedings of the Second International Symposium on Trichoptera. Junk, The Hague.

CAMERON, G. N., AND T. W. LAPOINT. 1978. Effects of tannins on the decomposition of Chinese Tallow leaves by terrestrial and aquatic invertebrates. Oecologia 32:349-366.

CLARKE, A.H. 1981. Introduction. Pages 41-42 in Proceedings of the Second American Malacological Union Symposium on the Endangered Molluscs of North America, Bulletin of the American Malacological Union, Incorporated, 1981.

COMIN, F. A., AND W. D. WILLIAMS. 1994. Parched continents: our common future? Pages 473-527 in R. Margalef (editor). Limnology now: a paradigm of planetary problems. Elsevier, Amsterdam.

DANKS, H. V. 1987. Insect dormancy: an ecological perspective. Biological Survey of Canada Monograph series No. 1., Biological Survey of Canada, Ottawa.

DUFFEY, E. 1968. Ecological studies on the large copper butterfly Lycaena dispar batavus Obth. at Woodwalton Fen National Nature Reserve, Huntingdonshire. Journal of Applied Ecology 5: 69-96.

References Cont.

EVANS, R.R. 2000. California Farm Bureau Federation, ag groups: fairy shrimp not threatened. Agriculture Alert http:/www.cfbf.com/archive/aa-1029c.htm

EVERARD, M, R. BLACKHAM, K. ROUEN, W. WATSON, A. ANGELL, AND A. HULL. 1999. How do we raise the profile of ponds? Freshwat Forum 12: 32-43.

FEDERAL REGISTER 1996. Final notice of issuance, reissuance and modification of nationwide permits. Army Corps of Engineers, DOD, Volume 61. p. 65916.

FERNANDO, C. H. 1958. The colonisation of small freshwater habitats by aquatic insects. I. General discussion, methods and colonisation in the aquatic Coleoptera. Ceylon Journal of Science (Biological Sciences) 1:117-154.

FERNANDO, C. H., AND D. F. GALBRAITH. 1973. Seasonality and dynamics of aquatic insects colonising small habitats. Verhandlungen der Internationalen Vereinigung fÄr theoretische und angewandte Limnologie 18:1564-1575.

FRY, L.L. AND M.S. MULLA. 1992. Effect of drying period and soil moisture on egg hatch of the tadpole shrimp (Notostraca: Triopsidae). Journal of Economic Entomology 85: 65-69.

GOETTLE, B. 2000. A ñliving fossilî in the San Francisco Bay Area? http:/ www.r1.fws.gov/sfbnwr/tadpole.html

HARPER, P. P., AND H. B. N. HYNES. 1970. Diapause in the nymphs of Canadian winter stoneflies. Ecology 51:425-427.

HARRISON, R. G. 1980. Dispersal polymorphisms in insects. Annual Review of Ecology and Systematics 11:95-118.

HENGEVELD, H.G. 1990. Global climate change: implications for air temerature and water supply in Canada. Transactions of the American Fisheries Society 119: 176-182.

HINTON, H. E. 1960. A fly larva that tolerates dehydration and temperatures of -270ž to +102ž C. Nature 186:336-337.

HOGG, I.D. AND D.D.WILLIAMS. 1996. Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. Ecology 77: 395-407.

HOGG, I.D., D.D.WILLIAMS, J.M. EADIE, AND S.A. BUTT. 1995. The consequences of global warming for stream invertebrates: a field simulation. Journal of Thermal Biology 20: 199-206.

HORSFALL, W. R. 1956. Eggs of floodwater mosquitoes. III. Conditioning and hatching of Aedes vexans (Diptera: Culicidae). Annals of the Entomological Society of America 49:66-71.

INGRAM, B. R. 1976. Life histories of three species of Lestidae in Northern Carolina, U.S. (Zygoptera). Odonatologica 5:231-244.

References Cont.

JEFFRIES, M. J. 1994. Invertebrate communities and turnover in wetland ponds affected by drought. Freshwater Biology 32:603-612.

JOHANSSON, F. 1993. Intraguild predation and cannibalism in odonate larvae: effects of foraging behaviour and zooplankton availability. Oikos 66:80-87.

JULIANO, S. A., AND T. L. STOFFREGREN. 1994. Effects of habitat drying on size at, and time to, metamorphosis in the tree hole mosquito Aedes triseriatus. Oecologia 97:369-376.

KIRKMAN, L.K., S.W. GOLLADAY, L. LACLAIRE, AND R. SUTTER. 1999. Biodiversity in southeastern, seasonally ponded, isolated wetlands: management and policy perspectives for research and conservation. Journal of the North American Benthological Society 18: 553-562.

LANDIN, J. 1980. Habitats, life histories, migration, and dispersal by flight of two water beetles, Helophorus brevipalpis and H. strigifrons (Hydrophilidae). Holarctic Ecology 3:190-201.

LEHMKHUL, D. M. 1973. A new species of Baetis from ponds in the Canadian Arctic, with biological notes. Canadian Entomologist 10:343-346.

LUSH, D. L. 1981. Organic carbon in aquatic ecosystems: beyond energy - control. Pages 141-154 in M. A. Lock and D. D. Williams (editors). Perspectives in running water ecology. Plenum Press, New York.

MACAN, T. T. 1939. Notes on the migration of some aquatic insects. Journal of the Society of British Entomologists 2:1-6.

MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

MAHER, M., AND S. M. CARPENTER. 1984. Benthic studies of waterfowl breeding habitats in south-western New South Wales. II. Chironomid populations. Australian Journal of Marine and Freshwater Research 35:97-110.

McLACHLAN, A. 1993. Can two species of midge coexist in a single puddle of rain-water? Hydrobiologia 259:1-8.

MOORE, N.W. 1976. The conservation of Odonata in Great Britain. Odonatologia 5: 37-44.

MOORE, N.W. 1980. Lestes dryas Kirby - a declining species of dragonfly (Odonata) in need of conservation: notes on its status and habitat in England and Ireland. Biological Conservation 17: 143-148.

MORIN, P. J., S. P. LAWLER, AND E. A. JOHNSON. 1988. Competition between aquatic insects and vertebrates: interaction strength and higher order interactions. Ecology 69:1401-1409.

NILSSON, A. N., AND B. W. SVENSSON. 1994. Dytiscid predators and culicid prey in two boreal snowmelt pools differing in temperature and duration. Annales Zoologiae Fennici 31:365-376.

POFF, N. L., AND J. V. WARD. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46:1805-1818.

RACKHAM, O. 1986. The History of the Countryside. J.M. Dent & Sons Ltd., London.

SCHNEIDER, D. W., AND T. M. FROST. 1996. Habitat duration and community structure in temporary ponds. Journal of the North American Benthological Society 15:64-86.

References Cont.

STANSBERY, D.H. 1971. Rare and endangered molluscs in the Eastern United States. Pages 117-124 in S.E. Jorgensen and R.W. Sharp (editors). Proceedings of a Symposium on Rare and Endangered Molluscs (Naiads). U.S. Department of the Interior, Fish and Wildlife Service.

SWEENEY, B.W., J.K. JACKSON, J.D.NEWBOLD AND D.H. FUNK. 1992. Climate change and the life histories and biogeography of aquatic insects in eastern North America. Pages 143-176 in P. Firth and S.G. Fisher (editors). Global Climate Change and Freshwater Ecosystems, Springer-Verlag, New York.

THIENEMANN, A. 1954. Chironomus. Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. BinnengewÉsser 20:1-834.

VALETT, H. M., S. G. FISHER, N. B. GRIMM, AND P. CAMILL. 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. Ecology 75:548-560.

WELLS, S.M., R.M. PYLE AND N.M. COLLINS. 1983. The International Union for Conservation of Nature and Natural Resources Invertebrate Red Data Book. IUCN, Gland, Switzerland.

WIGGINS, G. B., R. J. MACKAY, AND I. M. SMITH. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie (Supplement) 58:97-206.

WILLIAMS, D. D. 1983. The natural history of a nearctic temporary pond in Ontario with remarks on continental variation in such habitats. Internationale Revue der gesamten Hydrobiologie 68:239-254.

WILLIAMS, D. D. 1991. Life history traits of aquatic arthropods in springs. Pages 63-87 in D.D. Williams and H.V. Danks (editors). Arthropods of springs, with particular reference to Canada. Memoir of the Entomological Society of Canada, No. 155.

WILLIAMS, D. D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. Journal of the North American Benthological Society 15: 634-650.

WILLIAMS, D. D. 2002. Temporary water crustaceans: biodiversity and habitat loss. in E. Escobar-Briones and F. Alvares (editors). Modern Approaches to the Study of Crustacea. Kluwer Academic/Plenum Publishers, New York. (in press).

WILLIAMS, D. D., AND B.W. COAD. 1979. The ecology of temporary streams III. Temporary stream fishes in southern Ontario, Canada. Internationale Revue der gesamten Hydrobiologie 64: 501-515.

WILLIAMS, D. D., AND H. B. N. HYNES. 1976. The ecology of temporary streams I. The faunas of two Canadian streams. Internationale Revue der gesamten Hydrobiologie 61:761-787.

WILLIAMS, D. D., AND H. B. N. HYNES. 1977. The ecology of temporary streams II. General remarks on temporary streams. Internationale Revue der gesamten Hydrobiologie 62:53-61.

WOOD, D. M., P. T. DANG, AND R. A. ELLIS. 1979. The mosquitoes of Canada (Diptera: Culicidae). The insects and arachnids of Canada, Part 6. Agriculture Canada Publication 1686.

WRUBLESKI, D.A. 1987. Chironomidae (Diptera) of peatlands and marshes in Canada. Pages 141-161. in D.M. Rosenberg and H.V. Danks (editors). Aquatic Insects of Peatlands and Marshes in Canada. Memoir of the Entomological Society of Canada, No. 140.